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Effects of elevated CO_2 and drought on wheat: testing crop simulation models for different experimental and climatic conditions

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Abstract

Effects of increasing carbon dioxide concentration [CO_2] on wheat vary depending on water supply and climatic conditions, which are difficult to estimate. Crop simulation models are often used to predict the impact of global atmospheric changes on food production. However, models have rarely been tested for effects on crops of [CO_2] and drought for different climatic conditions due to limited data available from field experiments.

Simulations of the effects of elevated [CO_2] and drought on spring wheat (*Triticum aestivum* L.) from three crop simulation models (LINTULCC2, AFRCWHEAT2, Sirius), which differ in structure and mechanistic detail, were compared with observations. These were from 2 years of free-air carbon dioxide enrichment (FACE) experiments in Maricopa, Arizona and 2 years of standardised (in crop management and soil conditions) open-top chamber (OTC) experiments in Braunschweig and Giessen, Germany. In a simulation exercise, models were used to assess the possible impact of increased [CO_2] on wheat yields measured between 1987 and 1999 at one farm site in the drought prone region of Andalucia, south Spain.

The models simulated well final biomass (BM), grain yield (GY), cumulative evapotranspiration (ET) and water use efficiency (WUE) of wheat grown in the FACE experiments but simulations were unsatisfactory for OTC experiments. Radiation use efficiency (RUE) and yield responses to [CO_2] and drought were on average higher in OTC than in FACE experiments. However, there was large variation among OTC experiments. Plant growth in OTCs was probably modified by

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several factors related to plot size, the use (or not use) of border plants, airflow pattern, modification of radiation balance and/or restriction of rooting volume that were not included in the models. Variation in farm yields in south Spain was partly explained by the models, but sources of unexplained yield variation could not be identified and were most likely related to effects of pests and diseases that were not included in the models. Simulated GY in south Spain increased in the range between 30 and 65% due to doubling [CO_2]. The simulated increase was larger when a [CO_2] × drought interaction was assumed (LINTULCC2, AFRCWHEAT2) than when it was not (Sirius).

It was concluded that crop simulation models are able to reproduce wheat growth and yield for different [CO_2] and drought treatments in a field environment. However, there is still uncertainty about the combined effects of [CO_2] and drought including the timing of drought stress and about relationships that determine yield variation at farm and larger scales that require further investigation including model testing.

Keywords: Wheat; Crop simulation models; CO_2; Drought; Climatic conditions

1. Introduction

Limitation of water supply reduces wheat productivity in many parts of the world. Increased atmospheric CO_2 concentration, [CO_2], (IPCC, 2001) tends to increase wheat growth and yield (Kimball, 1983; Cure and Acock, 1986; Idso and Idso, 1994) more under drought conditions as compared with conditions with unlimited water supply (Kimball et al., 1995). This has been explained by the reduction in stomatal conductance and water use induced by [CO_2] elevation (Morison, 1985). Effects of [CO_2] on wheat also depend on weather conditions, e.g. temperature (Long, 1991; Morison and Lawlor, 1999). However, the overall understanding of the interactive effects of drought and [CO_2] on wheat in relation to climatic conditions is limited.

Crop simulation models are useful tools to account for the complexity of plant and crop responses to variation in water supply, [CO_2] and weather and are increasingly used to assess the possible impact on food production of future global change (e.g. Wolf, 1993; Rosenzweig and Parry, 1994; Downing et al., 2000). However, available models differ in structure and detail and use different approaches to simulate the effects of [CO_2], drought and weather on wheat. Experimental data to test these models for combined changes in water supply and [CO_2] in field environments are limited. Few data are available for wheat and refer to 2 years of free-air carbon dioxide enrichment (FACE) experiments performed in Maricopa, AZ (Kimball et al., 1995, 1999; Hunsaker et al., 1996; Pinter et al., 2000). Different models were tested with observations from these experiments (Kartschall et al., 1995; Grant et al., 1999; Tubiello et al., 1999). However, simulations from different models of the responses of wheat to [CO_2] and drought have rarely been tested and compared for a wider range of conditions.

Open-top chamber (OTC) facilities are less costly than FACE experiments and have been used mostly to study plant responses to ozone and other air pollutants (e.g. Heck et al., 1988; Skärby et al., 1993). More recently, OTCs were also used in multi-site experiments to study combined effects on wheat of elevated [CO_2] and ozone and/or water supply in relation to weather (Bender et al., 1999; Manderscheid et al., 2001). However, OTCs modify growing conditions, mainly through increases in air temperature and a reduction in incident solar radiation (Kimball et al., 1997; van Oijen et al., 1999). Few attempts have been made to use data from OTC experiments for testing crop models. Recently, simulations of the effects of [CO_2] and tropospheric ozone on wheat from crop simulation models were compared with data from a series of OTC experiments across Europe (Ewert et al., 1999; van Oijen and Ewert, 1999; Ewert and Porter, 2000). Even though simulations were performed using climate data measured within the OTCs only 25% of the variation in grain yield (GY) among sites and treatments could be explained by the models (van Oijen and Ewert, 1999). It was concluded that soil-related differences among sites, which were not considered in the models, affected water and nutrient relations causing additional variation in wheat growth and yield (Ewert et al., 1999; van Oijen and Ewert, 1999). However, it has not been tested yet whether standardised soils and controlled water supply reduce unexplained variability of wheat from OTC experiments.

Confidence in model predictions of the effects of global change on crops is based on their ability to reproduce plant responses obtained from experimental observations. In the absence of such data, understanding of differences in models behaviour for a wider range of conditions becomes particularly important. The present study aims (i) to test different crop models to simulate the effects on wheat of [CO_2] and drought for experiments in a field environment, (ii) to evaluate simulations for OTC experiments and (iii) to apply the different models in a simulation exercise to assess the potential effects of elevated [CO_2] on farm yields for a region where yield variation is mostly due to water availability. Three models, Sirius (Jamieson et al., 1998b) and modified versions of LINTULCC2 (Rodriguez and Goudriaan, 2000; Rodriguez et al., 2001) and AFRCWHEAT2 (Weir et al., 1984; Porter, 1993) were considered in this analysis. The models differ in structure and in detail and were chosen because (i) they represent different modelling approaches of CO_2 assimilation and (ii) they have simulated effects of [CO_2] (e.g. Jamieson et al., 2000; Wolf and Kempenaar, 1998) and water supply (e.g. Jamieson et al., 1998a) satisfactorily on field grown wheat in earlier studies. Data for model testing were taken from 2 years of FACE experiments performed at Maricopa, Arizona, with spring wheat *Triticum aestivum* L. cultivar Yecora Rojo and from 2 years of OTC experiments at two locations in Germany with spring wheat cultivar Minaret. In the OTC experiments, soil conditions and crop management were standardised and water supply was controlled. Effects of doubling CO_2 on farm yields were simulated for spring wheat cultivar Cartaya grown between 1987 and 1999 at one location in the region of Andalucia, south Spain.

2. Materials and methods

2.1. Model descriptions

The three models (LINTULCC2, AFRCWHEAT2 and Sirius) used in this analysis have routines to simulate phenological and canopy development, CO_2 assimilation and partitioning and soil water balance. The models have been described in detail several times (see the following sections). Thus, model description is restricted to the processes and relationships, which account for the effects of [CO_2] and drought on wheat growth and yield. Particular emphasise is on the differences among models to simulate CO_2 assimilation and on the parts of the models, which have been modified for this purpose.

LINTULCC2 (Rodriguez and Goudriaan, 2000; Rodriguez et al., 2001) simulates crop assimilation using detailed calculations of leaf energy balances and couples photosynthesis to stomatal conductance and root water uptake. LILTULCC2 uses a biochemical model of leaf photosynthesis (Farquhar et al., 1980) which is coupled with an equation for stomatal conductance (Leuning, 1995). Stomatal conductance is also reduced due to drought (Leuning et al., 1998). Canopy development is calculated as a function of air temperature and sink and source interactions (Rodriguez and Goudriaan, 2000; Rodriguez et al., 2001). Radiation is separated into direct, diffuse and near infrared radiation and intercepted by canopy layers (Goudriaan, 1990). Assimilation is simulated for sunlit and shaded leaves of each layer and integrated over the canopy (Rodriguez and Goudriaan, 2000; Rodriguez et al., 2001). In LINTULCC2, increase in [CO_2] will positively affect leaf photosynthesis and canopy size but will reduce stomatal conductance and transpiration (Rodriguez et al., 2001). Drought effects are accounted for by factors, which reduce leaf expansion and longevity, stomatal conductance and the light-saturated rate of photosynthesis. Drought factors are calculated from plant available water, which is calculated for a layered soil profile using relationships that describe downward root front velocity and the distribution of root length density (Monteith et al., 1989). Water uptake is the minimum of water availability calculated from a maximum uptake rate per unit root length (supply) and evaporative demand. The latter is calculated using the combination equation of Penman–Monteith (Monteith, 1981).

AFRCWHEAT2 simulates canopy development in more detail than the other two models—calculating leaf and tiller emergence, expansion, and senescence (Porter, 1984; Weir et al., 1984; Porter, 1993). However, light interception and photosynthesis and the effects of drought and [CO_2] on leaf photosynthesis and leaf area dynamics are simulated in less detail than with LINTULCC2. The canopy is divided into layers calculated in integer steps of green area index (GAI), and light interception is modelled as an exponential function of cumulative GAI from the top of the canopy (Charles-Edwards, 1978). Leaf assimilation is calculated using a non-rectangular hyperbolic function to simulate leaf photosynthesis in response to light with a relationship to account for variation in temperature (Weir et al., 1984). The maximum photosynthetic rate is determined by atmospheric CO_2 concentration and the combined physical resistances to [CO_2] uptake, including boundary, stomatal and mesophyll resistance (Weir et al., 1984). Atmospheric [CO_2] affects quantum efficiency, i.e. the initial slope of the photosynthesis–light response curve (Porter, 1993). A modification has been introduced to reduce crop transpiration linearly with [CO_2] elevation assuming a reduction in crop transpiration by 10% when [CO_2] is double current values (Goudriaan and Unsworth, 1990). Two factors are calculated from the ratio of water available for extraction and the demand for crop transpiration to account for the drought effects on tillering, leaf extension and senescence and photosynthesis (Porter, 1993). Soil water uptake is simulated as the lesser of evaporative demand and soil water supply, which is calculated from a layered soil profile using calculations of root front velocity and a root restriction factor based on root length density (Jamieson and Ewert, 1999). Potential evaporation was calculated using the Penman–Monteith equation (Monteith, 1965). Originally, AFRCWHEAT2 underestimated evapotranspiration (ET) in the well-watered (WW), ambient [CO_2] treatments in the FACE experiments, so the root restriction factor was modified to be less severe (Ritchie and Otter, 1985). However, it is as likely that the underestimation of ET was due to an underestimation of potential ET at the Maricopa FACE site (Tubiello et al., 1999; Section 2.3).

The simplest approach to simulate the effects of [CO_2] and drought on wheat growth and yield is taken by Sirius. Biomass (BM) production is calculated as the product of intercepted photosynthetically active radiation (IPAR) and radiation use efficiency (RUE), which is constant unless reduced under extreme water stress (Jamieson et al., 1998b). This approach was modified assuming that RUE increases linearly due to [CO_2] elevation so that doubling the ambient CO_2 concentration increases RUE by 30% (Jamieson et al., 2000). Radiation interceptance is related to GAI via Beer's law, and GAI is calculated as a function of thermal time (Jamieson et al., 1998b). GAI can be reduced due to drought, which is represented by one factor calculated from the accumulated difference between actual ET and precipitation plus soil water stored in the rooted soil volume (Jamieson et al., 1998b). In Sirius, elevated [CO_2] may increase GAI and enhance canopy senescence but does not reduce transpiration as it is considered in LINTULCC2 and AFRCWHEAT2. Thus, Sirius simulates [CO_2] effect on growth independent of water supply, which is different to the other two models (see the earlier sections). Potential evaporation is calculated using the Penman equation as formulated by French and Legg (1979) (Jamieson et al., 1998b). Unmodified, Sirius underestimated potential ET in the FACE experiments. Again, this is probably due to the arid and rather dry climate of the location (Tubiello et al., 1999) with substantial advective enhancement of ET in an irrigated field within a desert environment. Thus, simulations of potential ET in Sirius were corrected by a factor of 1.7 to account for this effect (Section 2.3).

The major time step of the three models is 1 day, except for the assimilation calculations in LINTULCC2 and AFRCWHEAT2, which are simulated hourly and integrated over a day. All simulations were performed using information about soil characteristics, water and nitrogen supply and data for temperature, radiation, rainfall/irrigation and CO_2 concentration measured in the FACE experiments, within the OTCs and at the field site in south Spain (Section 2.2) as input data. There were no limitation from nutrients or additional stresses due to pests and weeds in all simulations, which was consistent with experimental performance (Section 2.2).

2.2. Experimental

The data used to test simulations from all three models of the effects of [CO_2] and drought on wheat refer to FACE experiments performed near Maricopa, Arizona, in 1992/1993 and 1993/1994 and to OTC experiments performed in 1998 and 1999 in Braunschweig and Giessen, Germany. Experimental conditions and treatments in the FACE and OTC experiments are summarised in Table 1. More detailed descriptions of the FACE experiments are given in

Table 1
Summary description of growing conditions in FACE and OTC experiments considered in the present study

Site, geographic position	Year	Cultivar	Size of plots, subplots		Border plants	CO_2 (μmol mol^{-1})		Irrigation (mm)		T (°C)[a]	SRAD (MJ m^{-2} d^{-1})[b]	
			Diameter (m)[c]	Area (m^2)[d]		Low	High	WS[e]	WW[f]		AA[g]	OTC
FACE												
Maricopa	1992/1993	Yecora	25.0	–[d]	×	370	550	592[h]	919[h]	14.5	17.5	–
33°4′N and 111°59′W	1993/1994	Rojo	25.0	–[d]	×	370	550	278	629	13.8	18.9	–
OTC												
Braunschweig	1998	Minaret	3.1	0.79	×[i]	380	670	154	382[j]	15.1	13.9	10.0
52°18′N and 10°26′E	1999		3.1	3.1	×	410	680	169	427	14.2	16.3	12.4
Giessen	1998	Minaret	3.0	0.06	–	370	650	309[k]	598[k]	18.9	17.4	9.9
50°34′N and 8°40′E	1999		3.0	1.76	–	380	690	102	434	19.9	17.2	10.2

[a] Mean seasonal temperature from sowing to harvest maturity.
[b] Mean seasonal solar radiation from sowing to harvest maturity.
[c] Diameter of FACE rings and OTCs.
[d] Area of subplots or pots used in OTC experiments, FACE plots were split into two subplots (Hunsaker et al., 1996).
[e] Water-Stressed.
[f] Well-watered.
[g] Ambient air.
[h] Including an amount of 317 mm, which was given between sowing and emergence.
[i] Use of shading fences.
[j] Value refers to ambient CO_2 treatment, irrigation amount in the elevated CO_2 treatment was 324 mm.
[k] Value refers to ambient CO_2 treatments, irrigation amounts in the elevated CO_2 treatments were 316 and 596 mm for WS and WW, respectively.

Kimball et al. (1995, 1999), Hunsaker et al. (1996), and Pinter et al. (2000). CO_2 blowers caused some increase in air and canopy temperatures in the high [CO_2] treatments of the FACE experiments (Pinter et al., 2000) and this effect was not accounted for in the models. Detailed information about the performance of the OTC experiments can be obtained from Manderscheid et al. (2001). All OTC experiments were performed following a standard protocol including crop management and the use of a standard soil in all experiments (Cambisol, loamy sand with drained upper and lower limits of 0.20 and 0.04 $m^3\,m^{-3}$, respectively), (Manderscheid et al., 2001). However, there were differences among OTC experiments with respect to the size of the plots/subplots and whether or not border plants were grown in order to avoid penetration of horizontal light from the site into the plots (Table 1). Also, chambers absorbed between 20 and 45% of the incoming radiation depending on the experiment (Table 1). The FACE and OTC experiments were irrigated. Irrigation was reduced for plants in the drought treatments either via reduced amounts of irrigated water at each day of irrigation or via a reduced number of irrigation days, depending on the experiment (Hunsaker et al., 1996; Manderscheid et al., 2001). Nutrients were supplied to avoid additional stresses and pests and weeds were controlled as required in all FACE and OTC experiments. Information about measurements of final above ground BM, GY and cumulative ET considered in this analysis is given by Tubiello et al. (1999) for FACE and by Manderscheid et al. (2001) for OTC experiments. Water use efficiency (WUE) ($g\,mm^{-1}$) was calculated as the ratio of total above ground BM to cumulative ET.

Effects of doubling CO_2 on farm yields were simulated for spring wheat cultivar Cartaya grown between 1987 and 1999 at Montefrio (4°1′25″W and 37°18′45″N), Granada, Spain. Information about seasonal rainfall, mean seasonal temperature and solar radiation for this site is given in Table 2. There was no additional irrigation of plants to minimise effects of drought due to low rainfall. In all years crop management was to avoid additional stresses due to limitation of nutrient supply, pests and weeds. The soil at this site had drained upper limits and drained lower limits of 0.36 and 0.20 $m^3\,m^{-3}$, respectively within the top 0.30 m soil profile and 0.72 and 0.39 $m^3\,m^{-3}$ between 0.30 and 1.20 m.

Table 2
Seasonal averages of temperature and solar radiation and seasonal rainfall measured at Cordoba and Montefrio, Andalucia, Spain[a]

Year	T (°C)	Rainfall (mm)	Solar radiation ($MJ\,m^{-2}$ per day)
Cordoba			
1997/1998	15.2	293	16.7
Montefrio			
1987/1988	12.2	289	18.5
1988/1989	13.5	269	18.3
1989/1990	15.6	237	22.0
1990/1991	13.0	313	19.5
1991/1992	13.6	299	19.7
1992/1993	13.9	186	20.4
1993/1994	14.3	252	19.6
1995/1996	13.4	576	18.7
1996/1997	13.2	415	17.7
1997/1998	15.4	215	21.3
1998/1999	15.0	134	20.2

[a] Data were not available for Montefrio, 1994/1995.

2.3. Model calibration

Some calibration was required for all the models for the cultivars grown, and for the OTC experiments to account for the differences of the OTC experiments from field conditions. Sirius and AFRCWHEAT2 were calibrated using data from independent experiments at Maricopa in 1995/1996 (Jamieson et al., 2000). This calibration was confined to phenological development of the spring wheat cultivar Yecora Rojo. Further adjustments to the potential ET calculation were based on a comparison of predicted with observed ET from an independent WW, ambient CO_2 treatment in the 1992/1993 Maricopa experiment. For Sirius, the comparison was with energy balance measurements over a period of 65 days from February 1993, and calculated potential ET was increased by a factor of 1.7 to match observations. This modification was only applied to the FACE simulations. In the case of AFRCWHEAT2, the root restriction factor was adjusted to increase demand, and the change was retained in the OTC simulations. Calibration of LINTULCC2 for the FACE experiments used data from WW, ambient CO_2 treatment in 1992/1993. Measurements from the WW, ambient CO_2 treatment in Braunschweig 1998 were used to calibrate all three models for spring wheat cultivar Minaret grown in the OTC experiments. Originally, models underestimated

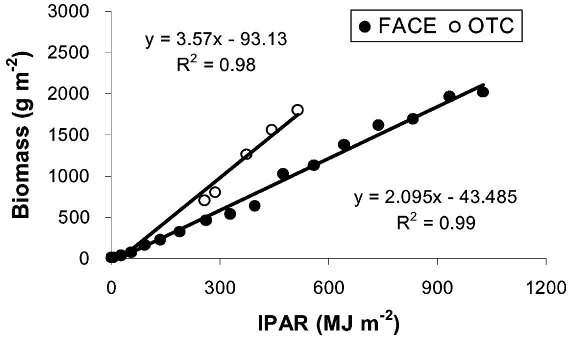

Fig. 1. Relationships between above ground BM and accumulated IPAR for the WW, low [CO_2] treatments from FACE (1992/1993) and OTC (Braunschweig in 1998) experiments.

wheat growth in the OTCs, which was due to the high RUE observed in all OTCs (Fig. 1). Thus, simulations of RUE were adjusted using the data from the WW, ambient CO_2 treatment in Braunschweig 1998.

Model calibration for spring wheat cultivar Cartaya grown in south Spain was performed using measurements of leaf emergence, GAI and final above ground BM and GY obtained from an independent field experiment at Cordoba, Andalucia, in 1997/1998 (see Table 2 for climatic conditions) without limitations of water and nutrient supply (Gomez et al., 1999). Calibration results for FACE and OTC experiments and for the cultivar grown in Spain are presented in Fig. 2.

2.4. Criteria for model comparison

Simulation results of development stages were evaluated using mean deviation (MD) and root mean square differences (RMSD) between simulated and observed data. A more advanced approach was taken to compare simulations of wheat growth and yield with observation. This approach is based on the mean square deviation (MSD) and its components: squared bias (SB), squared difference between standard deviations (SDSD) and lack of correlation weighted by the standard deviations (LCS) (Kobayashi and Salam, 2000). It was shown (Kobayashi and Salam, 2000) that

$$\mathrm{MSD} = \mathrm{SB} + \mathrm{SDSD} + \mathrm{LCS}$$

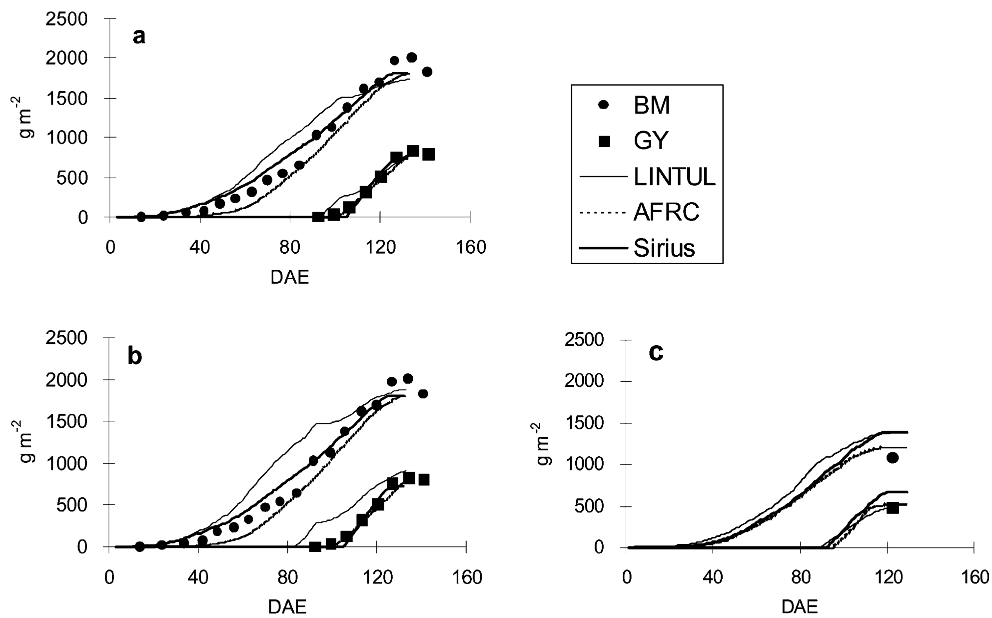

Fig. 2. Calibration results of LINTULCC2, AFRCWHEAT2 and Sirius for above ground BM and GY of spring wheat varieties observed in WW, ambient [CO_2] treatments at (a) Maricopa 1992/1993 (cultivar Yecora Rojo), (b) Braunschweig 1998 (cultivar Minaret) and (c) Cordoba (cultivar Cartaya), 1998. DAE, days after emeregence.

where $\mathrm{SB} = (\bar{x} - \bar{y})^2$, $\mathrm{SDSD} = (\mathrm{SD_s} - \mathrm{SD_m})^2$, and $\mathrm{LCS} = 2\mathrm{SD_s}\mathrm{SD_m}(1 - r)$, where

$$r = \frac{\left[(1/n)\sum(x_i - \bar{x})(y_i - \bar{y})\right]}{\mathrm{SD_s}\mathrm{SD_m}}$$

The terms $\mathrm{SD_s}$ and $\mathrm{SD_m}$ represent the standard deviations of x_i and y_i ($i = 1, \dots, N$), simulated and measured values, respectively. Advantages of this approach in comparison to the correlation–regression approach with the multiple criteria: correlation coefficient, the slope and the y-intercept of the regression line, which are often given in combination with RMSD and MD were demonstrated by Kobayashi and Salam (2000). The MSD approach indicates the overall deviation of model simulations. The MSD components, which are simply additive, represent different aspects of the overall deviation; MSD is equal to RMSD^2, SB represents the bias of the simulations and is equal to MD^2, SDSD indicates the difference in the variation of simulated and measured data and LCS gives information of how the pattern of variation in the measurements was simulated (Kobayashi and Salam, 2000).

3. Results and discussion

3.1. Observations from FACE and OTC experiments

In all FACE and OTC experiments wheat BM and GY were increased due to $[CO_2]$ elevation (Table 3). Limitation in water supply caused acceleration in phenological development and decrease in BM and GY. Cumulative ET was lower in the drought compared to the WW treatments and there was some reduction in

Table 3
Dates of anthesis (An) and maturity (Ma), and final above ground BM, GY, ET and WUE for BM measured in ambient (L) and elevated $[CO_2]$ (H) treatments under WW and WS conditions of experiments considered in the present analysis

Experiment	Treatment		An (DOY)[a]	Ma (DOY)[a]	BM ($\mathrm{g\,m^{-2}}$)	GY ($\mathrm{g\,m^{-2}}$)	ET (mm)	WUE ($\mathrm{g\,mm^{-1}}$)
	Water	CO_2						
Maricopa 1992/1993	WW	L	85	133	1960	825	625	3.1
	WW	H	83	126	2156	900	598	3.6
	WS	L	84	126	1528	648	457	3.3
	WS	H	81	124	1721	759	479	3.6
Maricopa 1993/1994	WW	L	96	141	1893	804	659	2.9
	WW	H	92	137	2022	862	623	3.2
	WS	L	93	133	1348	605	435	3.1
	WS	H	91	130	1583	724	439	3.6
Braunschweig 1998	WW	L	151	216	1801	836	402	4.5
	WW	H	151	216	1991	875	344	5.8
	WS	L	151	208	1201	512	224	5.4
	WS	H	151	208	1763	755	224	7.9
Braunschweig 1999	WW	L	158	195	1842	901	452	4.1
	WW	H	158	195	2068	1014	449	4.6
	WS	L	155	205	960	434	234	4.1
	WS	H	155	205	1392	654	239	5.8
Giessen 1998	WW	L	173	214	1525	790	553	2.8
	WW	H	173	214	2103	1107	548	3.8
	WS	L	173	209	845	401	321	2.6
	WS	H	173	209	1337	657	318	4.2
Giessen 1999	WW	L	185	235	1407	566	440	3.2
	WW	H	185	235	1850	832	435	4.3
	WS	L	183	224	1249	529	127	9.8
	WS	H	183	224	1373	647	124	11.1

[a] Day of the year.

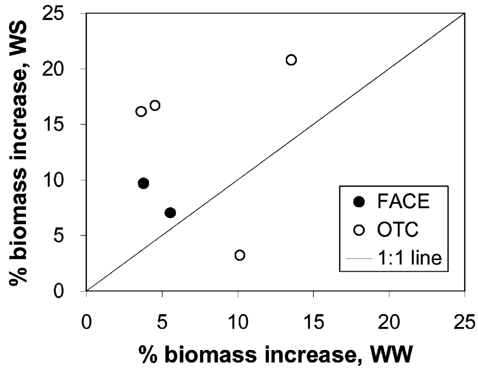

Fig. 3. Observed increase in BM (% of ambient [CO_2] treatments) per 100 μmol mol^{-1} increase in [CO_2] of spring wheat in WS vs. WW treatments from FACE (closed symbols) and OTC (open symbols) experiments.

ET under elevated [CO_2] in the WW treatments in all experiments.

However, there were some differences in wheat growth and development between both types of experiments. Phenological development was enhanced by few days due to [CO_2] elevation in the FACE experiments (Table 3). However, this was primarily due to an artefact of the CO_2 blowers that caused about 1 °C elevation of night-time air and canopy temperatures (Pinter et al., 2000). There were no differences in the air-flow pattern between CO_2 treatments in the OTC experiments and no effect of elevated [CO_2] on phenological development was observed.

Effects of [CO_2] on BM and GY were more pronounced in the OTC as compared to FACE experiments (Tables 3 and 5). This was only partly explained by the differences in the gas concentrations in the high [CO_2] treatments between OTCs (about 680 μmol mol^{-1} CO_2) and FACE (about 550 μmol mol^{-1} CO_2), (Table 1). Further analysis indicated that the relative increase in final BM and GY (not shown) per 100 μmol mol^{-1} increase in [CO_2] was about 4.7 and 8.3% for the WW and water-stressed (WS) treatments, respectively in the FACE experiments (Fig. 3). This was only half the relative increase observed in the OTCs (about 8.0 and 13.9% for WW and WS conditions, respectively, Fig. 3). Also, there was a substantial scatter in the responses of wheat to [CO_2] and drought in OTC experiments (Fig. 3).

ET was higher in the FACE compared to the OTC experiments, which was probably due to the arid and dry climate of the FACE location (Tubiello et al., 1999) and the longer growing season of cultivar Yecora Rojo compared to cultivar Minaret grown in the FACE and OTC experiments, respectively. Since there was little difference in final BM between the two types of experiments, calculated WUEs were higher for OTC compared to the FACE experiments.

3.2. *Simulations for FACE experiments*

3.2.1. *Phenology*

The phenological stages of anthesis and maturity were simulated reasonable well for the FACE experiments with little differences among models (Table 4). Simulations of anthesis and maturity in the FACE experiments were less accurate for AFRCWHEAT2 compared with the other two models. This was primarily because the model did not simulate acceleration in phenological development with water stress as observed in the FACE experiments and simulated by the other two models. Dates of anthesis and maturity were reached earlier in the elevated [CO_2] treatments

Table 4
Mean differences (MD, days) and RMSD (days) between simulated and observed dates of anthesis and maturity for FACE and OTC experiments considered in this study using three simulation models, LINTULCC2, AFRCWHEAT2 and Sirius[a]

Type of experiment	Parameter	Anthesis			Maturity		
		LINTUL	AFRC	Sirius	LINTUL	AFRC	Sirius
FACE	MD	1.9	5.9	3.9	0	7.25	2
	RMSD	5.5	7.2	5.1	4.6	8.2	4.6
OTC	MD	−2.6	−1.1	−1.9	3.06	−1.8	−6.9
	RMSD	4.9	3.1	5.3	7.3	7.8	9.8

[a] Values represent averages of all [CO_2] and water treatments.

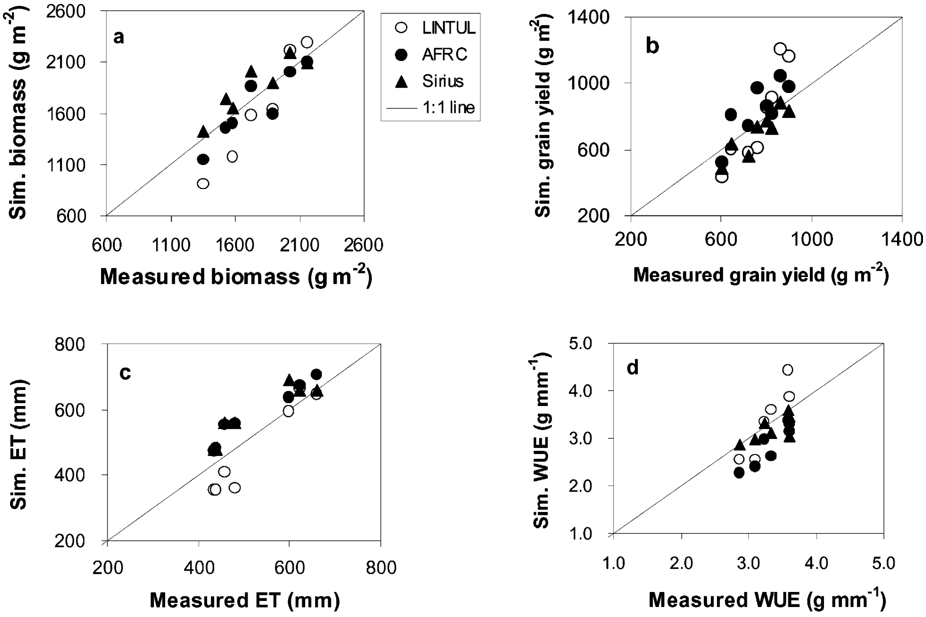

Fig. 4. Comparison of simulated (LINTULCC2, AFRCWHEAT2 and Sirius) with measured (a) final above ground BM, (b) GY, (c) cumulative ET and (d) WUE for BM of spring wheat cultivar Yecora Rojo subjected to four treatments (ambient and elevated [CO_2], WW and WS) in two FACE experiments at Maricopa in 1992/1993 and 1993/1994. Data from the WW, ambient [CO_2] treatment in 1992/1993 were used for model calibration (Fig. 2) and are not included.

compared to the ambient plots (Table 3). However, as indicated earlier this was primarily due to an artefact of the CO_2 blowers (Pinter et al., 2000). There was little evidence that [CO_2] effects on stomatal conductance and leaf temperature affected phenological development of wheat grown in the FACE experiments (Pinter et al., 2000). Since no adjustments were made in the models to account for the blower effect, differences between [CO_2] treatments were not simulated, which explains some of the differences between observed and simulated dates of anthesis and maturity in the FACE experiments (Table 4).

3.2.2. Final biomass and grain yield

Final BM and GY were simulated close to observed values by all three models (Fig. 4), although agreement between simulated and observed data was better for final BM than for GY (Fig. 4). Differences among models were only small. MSD between simulated and observed BM and GY were slightly higher for LINTULCC2 as compared to AFRCWHEAT2 and Sirius (Fig. 5). This was mainly due to high SDSD values for LINTULCC2 (Fig. 5). The model simulated more variation in final BM and particularly in GY among years and treatments than was observed (Figs. 4 and 5).

3.2.3. Evapotranspiration and water use efficiency

All three models simulated cumulative ET and WUE satisfactorily for the FACE experiments (Fig. 4). MSD values for ET and WUE were similar for all models (Fig. 5). However, some differences among models became evident from the analysis of MSD components. Again, LINTULCC2 simulated more variation in ET and WUE among years and treatments than was observed, as indicated by higher SDSD values compared to the other two models (Fig. 5). In contrast, MSD values for AFRCWHEAT2 and Sirius were primarily determined by SB values (Fig. 5). Both models slightly overestimated average observed ET, which also explains that observed WUE was slightly underestimated by the two models (Figs. 4 and 5).

3.2.4. Interaction between [CO_2] and drought

All three models overestimated [CO_2] effects on BM and GY particularly in the WW treatments

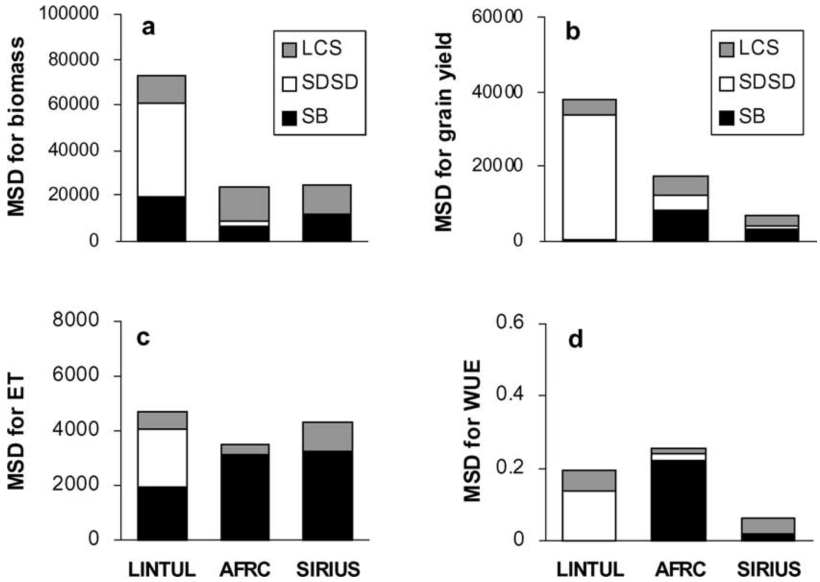

Fig. 5. MSD and its components: SB, SDSD and LCS calculated from the simulations of (a) final above ground BM, (b) GY, (c) cumulative ET and (d) WUE with LINTULCC2, AFRCWHEAT2 and Sirius presented in Fig. 4.

(Table 5). Additional effect of [CO_2] blowers on canopy development, which partly offset the [CO_2] effect in the FACE experiments (Pinter et al., 2000) and which were not considered in the models, might provide some explanation for this overestimation. Experimental data suggest that the stimulatory effects of elevated [CO_2] were more pronounced under drought than under WW conditions (Table 5). LINTULCC2 and AFRCWHEAT2 explicitly contain interaction between [CO_2] and water supply and, therefore, reproduced the observed interaction between [CO_2] × drought (Table 5). No such interaction between [CO_2] × drought is included in Sirius. Thus, Sirius simulated the same [CO_2] effects for WW and drought conditions. Interestingly, the differences among models about whether or not an effect of [CO_2] on water use is assumed had little impact on the accuracy of models simulations for the FACE experiments (Figs. 4 and 5). Again, it is possible that [CO_2] × drought interaction in the FACE experiment was partly offset by the CO_2 blowers which additionally increased air and canopy temperatures, and which in turn enhanced crop development and reduced final GY in the high CO_2 treatments (Pinter et al., 2000);

Table 5
Observed and simulated [CO_2] effects (elevated/ambient) on final above ground BM and GY for WW and WS treatments of wheat grown in FACE an OTC experiments

Type of experiment variable	Observed		LINTULCC2		AFRCWHEAT2		Sirius	
	WW	WS	WW	WS	WW	WS	WW	WS
FACE								
BM	1.08	1.15	1.19	1.29	1.25	1.30	1.16	1.16
GY	1.08	1.18	1.18	1.34	1.20	1.31	1.16	1.16
OTC								
BM	1.23	1.40	1.25	1.33	1.18	1.25	1.25	1.25
GY	1.26	1.46	1.26	1.47	1.17	1.24	1.25	1.25

an effect not accounted for in the models. On the other hand, this effect was again offset by reductions in cumulative ET associated with the reduced growth duration. So the significance of [CO_2] effects on transpiration in the field remains unclear, but is likely to be small.

3.3. Simulations for open-top chamber experiments

Phenological development of wheat grown in OTC experiments was simulated reasonably well with all three models (Table 4). However, there was a large scatter between simulations and observations for final BM, GY, cumulative ET and WUE for AFRCWHEAT2 (Fig. 6), LINTULCC2 and Sirius (not shown). Effects of [CO_2] on wheat BM and GY were higher in the OTC as compared to the FACE experiments and were underestimated by the models, particularly with AFRCWHEAT2 and Sirius (Table 5). Since simulations were generally unsatisfactory (Fig. 6) one model (AFRCWHEAT2) was used to identify possible sources for unexplained variability in wheat growth and yield from OTC experiments.

3.4. Variability of OTC experiments

Although models were adjusted to account for high RUE observed in the OTCs (Fig. 1) there was a variation in RUE among experiments, which was negatively related to the plot size (Fig. 7a). However, it should be noted that RUE was calculated from measured LAI and radiation above the canopy assuming a constant light extinction coefficient. Thus, effects of lateral light were not accounted for. It is likely that lateral light increased with decreasing plot size and that more light was intercepted in smaller plots. However, such relationships were not considered in the models and simulations were particularly unsatisfactory when plants were grown in small pots (Fig. 7b).

Effects of [CO_2] on BM and GY were higher in the OTC as compared to the FACE experiments and varied among OTC experiments (Section 3.1, Fig. 3). Further analysis suggested that wheat responses to [CO_2] were particularly high when plants were grown in small plots and/or without border plants or shading fences (Fig. 8a). Again, such relationships were not considered in the models and explained part of

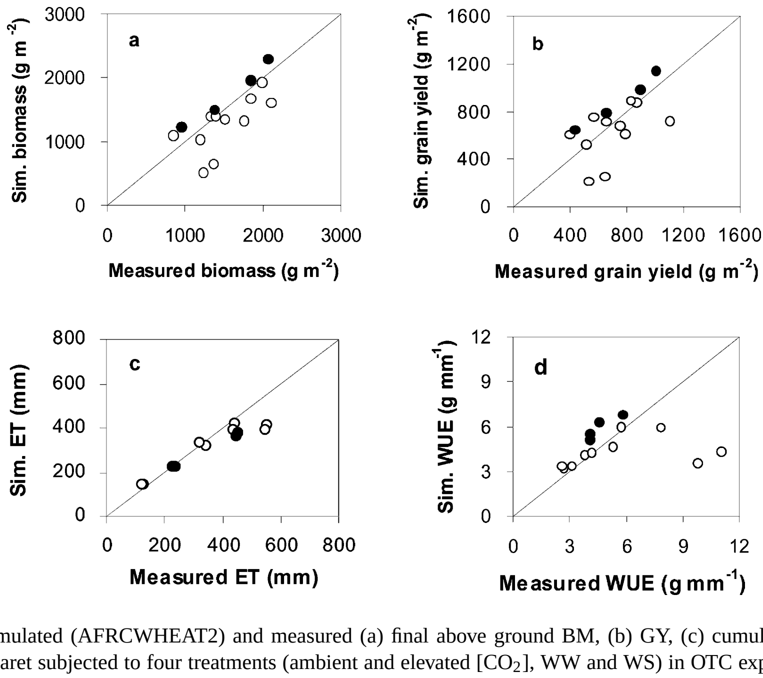

Fig. 6. Comparison of simulated (AFRCWHEAT2) and measured (a) final above ground BM, (b) GY, (c) cumulative ET and (d) WUE of spring wheat cultivar Minaret subjected to four treatments (ambient and elevated [CO_2], WW and WS) in OTC experiments at Braunschweig and Giessen in 1998 and 1999. Data from the WW, ambient [CO_2] treatment in Braunschweig 1998 were used for model calibration (Fig. 2) and are not included. Closed symbols represent the experiment in Braunschweig 1999, with plants grown in large plots and surrounded by border plants (see text and Table 1 for explanation).

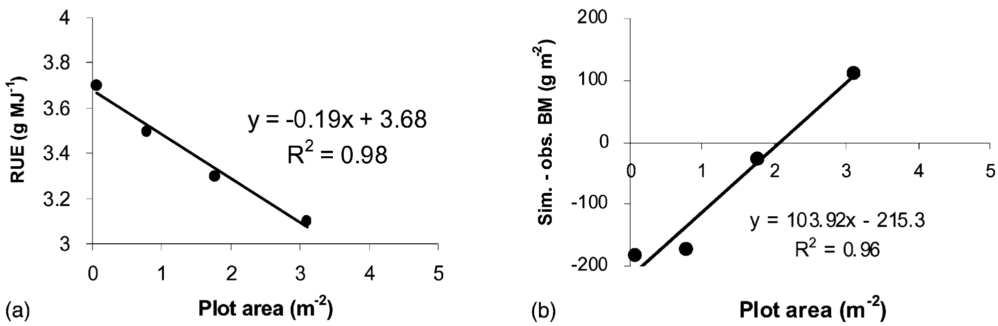

Fig. 7. Relationships between (a) observed RUE and plot area and (b) differences between simulated and observed final BM and plot area for WW, low [CO_2] treatments of OTC experiments in Braunschweig and Giessen in 1998 and 1999.

the deviation of model simulations from observed data (Fig. 8b).

Cumulative ET was underestimated by Sirius and by the original, unmodified version of AFRCWHEAT2 (not shown). In the models, potential ET (PET) is calculated using well-validated Penman (Sirius) or Penman–Monteith (AFRCWHEAT2) equations (e.g. Jamieson et al., 1998a; Jamieson and Ewert, 1999). However, these equations were developed for field conditions and might not represent the microclimatic conditions within OTCs. For instance, OTC plots were relatively small and there was constant mixture and movement of air through the canopy. Thus, crop boundary resistance was always small, which is different to field crops. It is also known that long-wave radiation is increased in OTCs compared to outside conditions (see Kimball et al., 1997) and is not detected by radiometers. On the other hand, the rooting volume was restricted in most experiments, which might have decreased root resistance and increased water uptake and transpiration. Simulations with the modified version of AFRCWHEAT2 (i.e. reduced root restriction, see Section 2.3) closely simulated observed average ET (not shown) but variation in ET was reproduced satisfactory only for some experiments (Fig. 6c). This indicates that modification of soil water balance due to OTCs can differ depending on the performance of the individual experiment.

There was some indication that wheat BM and GY were simulated more closely for OTC experiments in which plants were grown in large plots and surrounded by border plants or shading fences and when light absorption by chamber cover material was low (Fig. 6). This is consistent with Rodriguez et al.

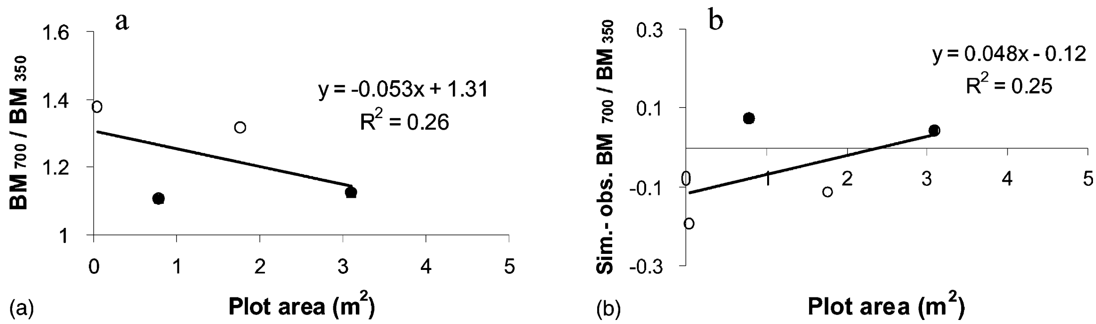

Fig. 8. Relationships between (a) observed [CO_2] effects on final BM and plot area, and (b) differences between simulated and observed [CO_2] effects on final BM and plot area for WW treatments of OTC experiments in Braunschweig and Giessen in 1998 and 1999. Closed and open symbols refer to experiments with or without border plants, respectively.

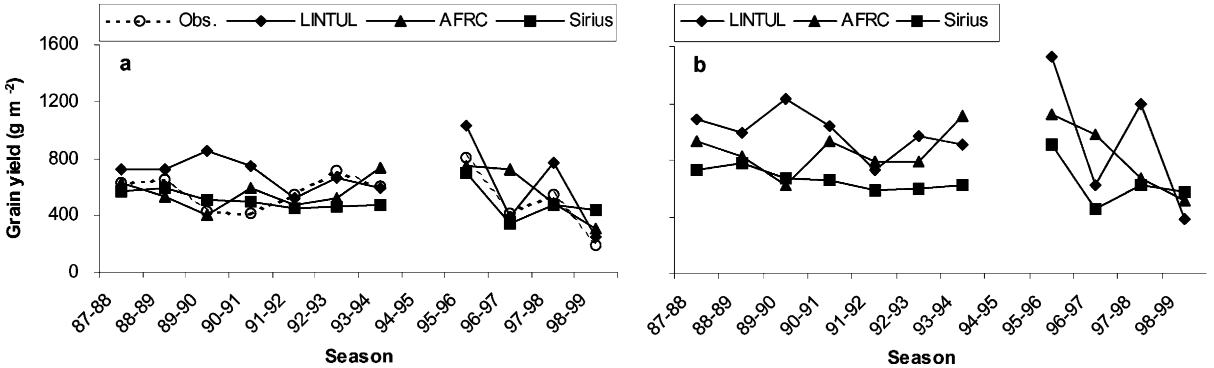

Fig. 9. Observed farm yields of spring wheat cultivar Cartaya at Montefrio, Andalucia, Spain, between 1987 and 1999 and simulated (LINTULCC2, AFRCWHEAT2, Sirius) GYs for (a) ambient [CO_2] and (b) 2 × ambient [CO_2]. Data for the 1994/1995 season were not available.

(2001) demonstrating that crop models can reproduced canopy assimilation well for plants grown in OTC experiments performed under these conditions.

3.5. Simulations of [CO_2] effects on farm yields

3.5.1. Simulations for ambient conditions

Spring wheat cultivar Cartaya was simulated between 1978 and 1999 at Montefrio (Granada), south Spain, for ambient conditions (350 μmol mol^{-1} CO_2) and simulations were compared with observed farm yields (Fig. 9a). Predicted yields agreed well with observations in only some years. In most years, yields were either overestimated or underestimated. Overestimation of yields by all three models might provide indication for some additional management effects related to the control of pests and diseases, etc.—factors not considered in the models. However, there were also differences among models. LINTULCC2 predicted some much higher yields than observed (Fig. 9a) and SB was highest for this model (Fig. 10). Some of these overestimations were associated with unsatisfactory predictions of anthesis date, which marks a period of great sensitivity to drought in wheat (Fischer, 1985). Sirius simulated less variation in GY among years than observed (Fig. 9a) which is also indicated by the high SDSD value for this model (Fig. 10). However, the overall MSD was lowest for Sirius. All models had problems reproducing the observed pattern in the variation of GY among years (see LCS values, Fig. 10). Other studies have also reported problems in reproducing observed variation in farm (Mitchell et al., 2001a) and regional yields (Landau et al., 1998; Mitchell et al., 2001a) with mechanistic crop models. However, it has been argued whether observed yield variations can be attributed only to known physiological effects that are included in the models (Jamieson et al., 1999). Other factors related to pests, diseases, etc. that models do not account for might play a more important role in determining such yield variations (Jamieson et al., 1999; Landau et al., 2000). Such factors may also have affected wheat growth and yield in the present study. This might also explain the observed weak relationship between GY and seasonal rainfall ($R^2 = 0.21$, Fig. 11a), although rainfall was low in several years (Table 2). On the other hand wheat varieties grown in this region show some adaptation to the dry growing conditions often experienced in late spring through to summer, e.g. spring wheat cultivar Cartaya grown in Cordoba between 1997 and 1999 reached anthesis

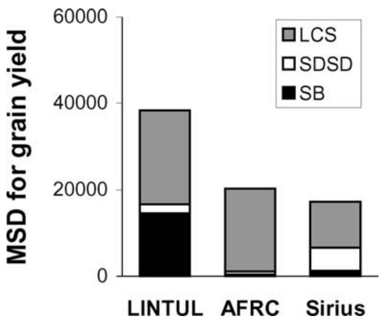

Fig. 10. MSD and its components: SB, SDSD and LCS between observed and simulated GYs from all seasons presented in Fig. 9a.

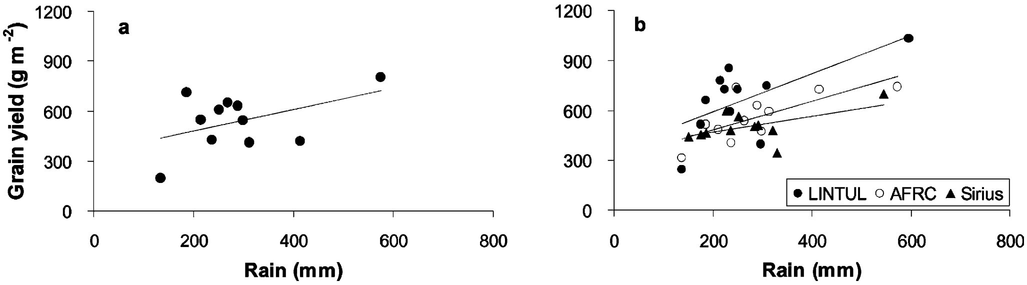

Fig. 11. (a) Observed and (b) simulated relationships between GY and seasonal rainfall of spring wheat cultivar Cartaya at Montefrio, Andalucia, Spain, between 1987 and 1999. The fitted regressions are of the form $y = a + bx$. The values for a and b are for observed, 0.647, 351.9 ($R^2 = 0.21$, $P = 0.15$); LINTULCC2, 1.142, 363.3 ($R^2 = 0.41$, $P = 0.033$); AFRCWHEAT2, 0.861, 311.7 ($R^2 = 0.53$, $P = 0.011$) and Sirius, 0.472, 374.5 ($R^2 = 0.30$, $P = 0.08$).

about 2–3 weeks earlier than spring wheat cultivar Minaret and drought effects on yield were less for cultivar Cartaya than for cultivar Minaret (Fereres et al., 2001). All three models were calibrated to account for the early development of cultivar Cartaya (Section 2.3). However, relationships between GY and rainfall were more significant from models simulations compared to observations with only small differences among models (Fig. 11b) suggesting that other factors not included in the models might have affected wheat growth and yield observed at this location.

3.5.2. Simulations for elevated [CO_2]

The simulations were repeated assuming a doubling of the atmospheric CO_2 concentration (700 μmol mol^{-1} CO_2), (Fig. 9b). Simulated GY increased due to doubling [CO_2] between 30 and 65% depending on year and model (not shown). Simulations with LINTULCC2 and AFRCWHEAT2 suggested that GY would increase on average over all years by about 50%, due to doubling [CO_2] (Fig. 12), which however, would vary depending on the year (Figs. 9b and 12). No interaction between [CO_2] and drought was assumed in Sirius and a smaller increase in GY (30%) due to high [CO_2] was simulated by the model with no variation among years (Fig. 12). In LINTULCC2 and AFRCWHEAT2 transpiration is reduced by increased [CO_2]. However, simulated variation in wheat responses to doubling [CO_2] from both models was not related to seasonal rainfall (Fig. 13) suggesting that the [CO_2] $\times$ drought interaction on wheat yield may depend on other factors such as the timing of drought stress. Investigations in OTC and

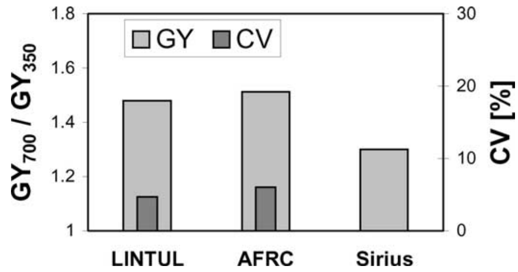

Fig. 12. Average simulated [CO_2] effects on GY and corresponding coefficient of variation (CV) for spring wheat cultivar Cartaya between 1987 and 1999 at Montefrio, Andalucia, Spain.

controlled environment experiments have shown that canopy photosynthesis of wheat was stimulated by elevated [CO_2] more under pre-anthesis drought conditions compared to WW controls, but the stimulation

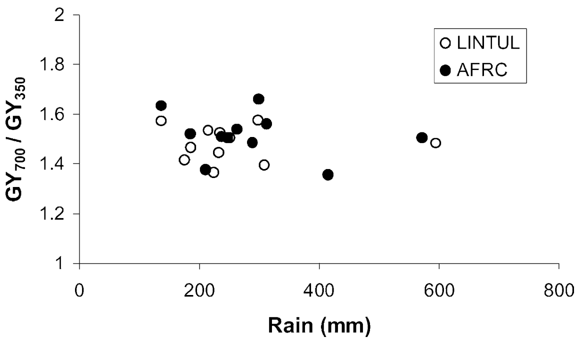

Fig. 13. Simulated [CO_2] effects on GY vs. seasonal rainfall for spring wheat cultivar Cartaya between 1987 and 1999 at Montefrio, Andalucia, Spain.

was the same for late-drought conditions and WW controls (Manderscheid et al., 2001; Mitchell et al., 2001b), which was also evident from simulations (not shown).

Importantly, differences in simulated yield increases due to doubling [CO_2] among models were small in comparison to the differences between simulated and between simulated and observed yields for ambient conditions. In some years, the differences between observed and simulated yields were even larger than simulated yield increase due to doubling [CO_2] (Fig. 9).

4. Conclusions

Simulations from different crop models of wheat responses to [CO_2] and drought were in good agreement with observations from field experiments. This confirms results from other simulation studies for the same experiments (Kartschall et al., 1995; Grant et al., 1999; Tubiello et al., 1999) and other experiments at the same site where *N* was the limiting factor (Jamieson et al., 2000), demonstrating that crop models can mimic wheat responses to [CO_2] in a field environment.

However, models differed about whether or not an effect of [CO_2] on water use was assumed. This had consequences on simulated effects of doubling [CO_2] on farm yields at a site with low seasonal rainfall. Effects of [CO_2] on yield were higher when a [CO_2] $\times$ drought interaction was assumed (LINTULCC2, AFRCWHEAT2) than when it was not (Sirius). However, the significance of an interaction between [CO_2] and drought including the timing of stress due to drought remains unclear and experimental data are required to test these effects for a field environment.

Model testing against data from OTC experiments performed at two locations in 2 years provided little additional information about the validity of the different modelling approaches. Although simulations were performed using climate data measured within OTCs to account for the chamber-induced modification of air temperature and radiation (Kimball et al., 1997; van Oijen et al., 1999) a substantial proportion of observed variation in wheat growth and yield remained unexplained. Standardisation in soil conditions and controlled water supply did not necessarily improve simulations of wheat grown in OTCs as suggested by Ewert et al. (1999) and van Oijen and Ewert (1999). Plant growth in OTCs was modified by several other factors related to plot size, the use (or not use) of border plants, airflow pattern, modification of radiation balance and/or restriction of rooting volume, in ways that are not well understood. However, quantitative understanding of such effects is required to conclude from the observations from experiments conducted in OTCs for field conditions.

Mechanistic simulation of observed yield variation at farm and larger scales remains difficult. Relationships that determine these variations are not well understood and are often dominated by factors such as pests and diseases that are not included in crop models. Results from the present study suggest that yield responses to [CO_2] and drought at higher levels of spatial scale are less understood than physiological relationships that determine wheat responses to [CO_2] and drought.

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